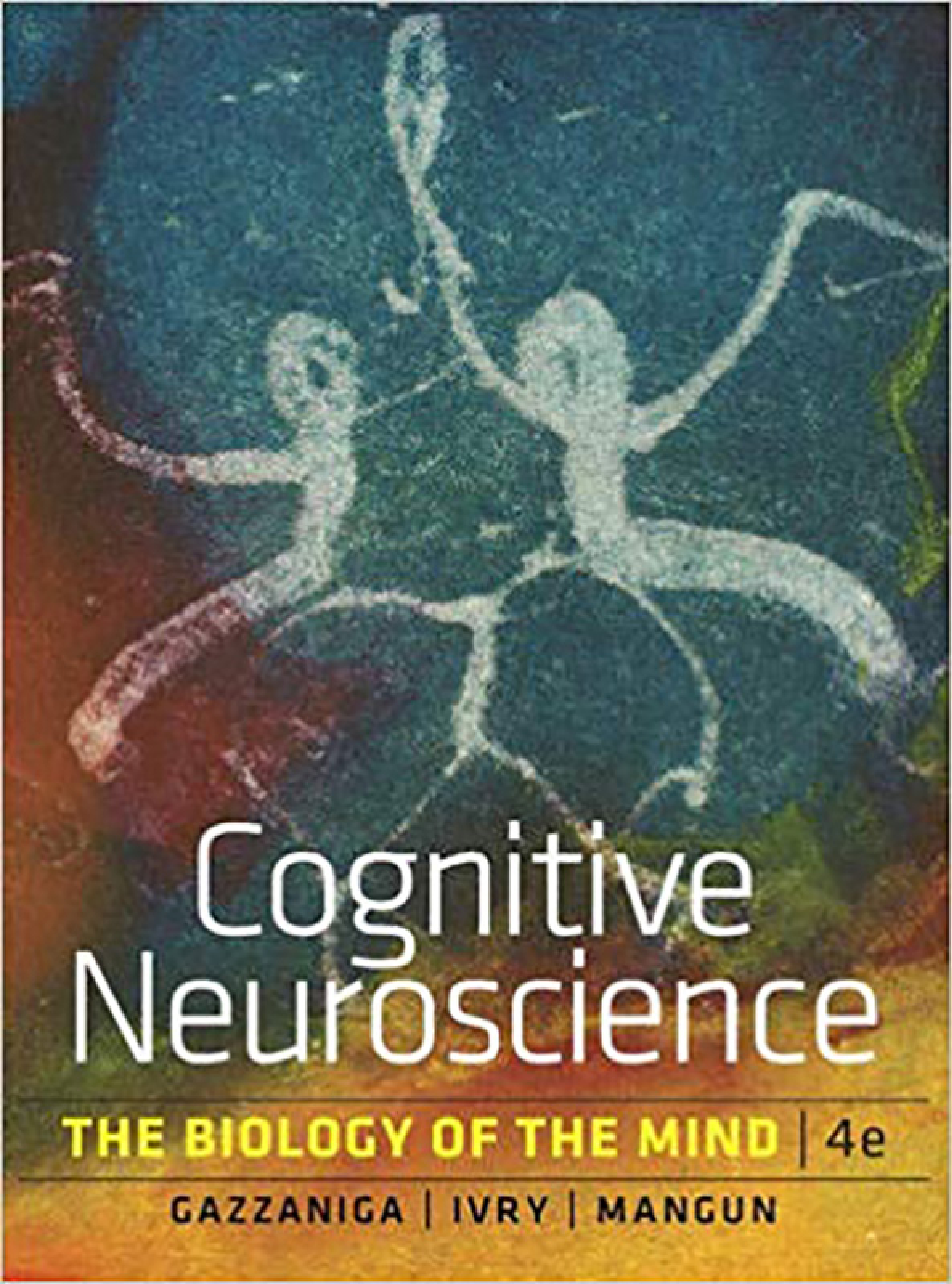

Cognitive Neuroscience

THE BIOLOGY OF THE MIND | 4e

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COGNITIVE NEUROSCIENCE
THE BIOLOGY OF THE MIND

Fourth Edition

Michael S. Gazzaniga, Richard B. Ivry, and George R. Mangun

FOURTH EDITION

Cognitive Neuroscience

The Biology of the Mind

MICHAEL S. GAZZANIGA
University of California, Santa Barbara

RICHARD B. IVRY
University of California, Berkeley

GEORGE R. MANGUN
University of California, Davis

With special appreciation for the Fourth Edition to Rebecca A. Gazzaniga, M.D.

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For Lilly, Emmy, Garth, Dante, and Rebecca
M.S.G.

For Henry and Sam
R.B.I.

For Nicholas and Alexander
G.R.M.

Brief Overview

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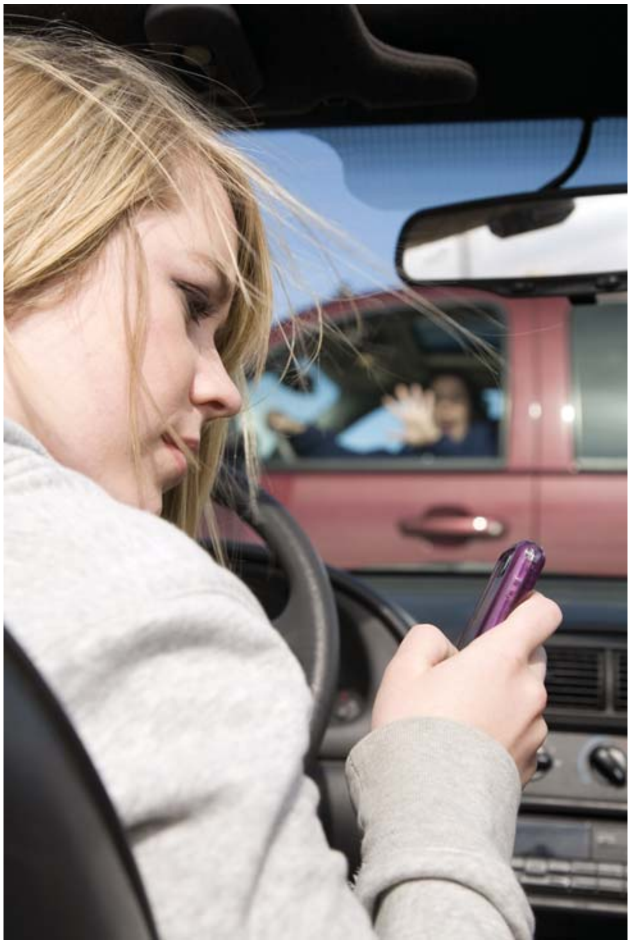

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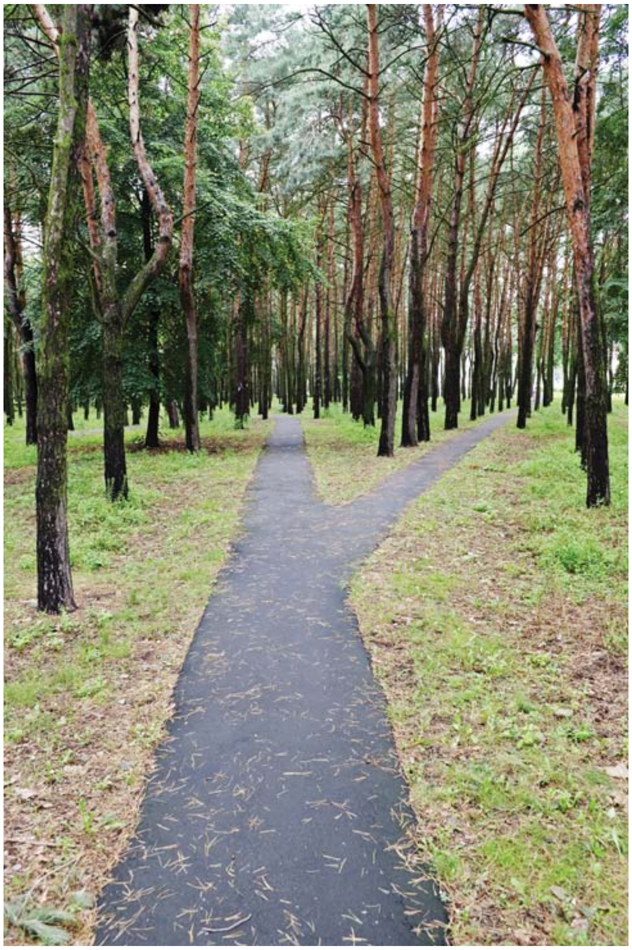

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Preface

Welcome to the fourth edition! When cognitive neuroscience emerged in the late 1970's, it remained to be seen if this new field would have "legs." Today, the answer is clear: the field has blossomed in spectacular fashion. Cognitive neuroscience is well represented at all research universities, providing researchers and graduate students with the tools and opportunities to develop the interdisciplinary research programs that are the mainstay of the field. Multiple journals, some designed to cover the entire field, and others specialized for particular methodologies or research themes, have been launched to provide venues to report the latest findings. The number of papers rises at an exponential rate. The annual meeting of the Cognitive Neuroscience Society has also flourished. While 400 pilgrims attended the first meeting in 1993, the 20th anniversary meeting in 2013 was attended by almost 2000 people.

The fundamental challenge we faced in laying the groundwork for our early editions was to determine the basic principles that make cognitive neuroscience distinct from physiological psychology, neuroscience, cognitive psychology, or neuropsychology. It is now obvious that cognitive neuroscience overlaps with, and synthesizes, these disciplinary approaches as researchers aim to understand the neural bases of cognition. In addition, however, cognitive neuroscience is increasingly informing and informed by disciplines outside the mind-brain sciences, as exemplified by our new Chapter 14: "Consciousness, Free Will, and the Law"

As in previous editions, we continue to seek a balance between psychological theory, with its focus on the mind, and the neuropsychological and neuroscientific evidence about the brain that informs this theory. We make liberal use of patient case studies to illustrate essential points and observations that provide keys to understanding the architecture of cognition, rather than providing an exhaustive description of brain disorders. In every section, we strive to include the most current information and theoretical views, supported by evidence from the cutting-edge technology that is such an important part of cognitive neuroscience. In contrast to purely cognitive or neuropsychological approaches, this text emphasizes the convergence of evidence that is a crucial aspect of any science, particularly studies of higher mental function. We also provide examples of research using computational techniques to complete the story.

Teaching students to think and ask questions like cognitive neuroscientists is a major goal of our text. As cognitive neuroscientists, we examine mind–brain relationships with a wide range of techniques, such as functional and structural brain imaging, neurophysiological recording in animals, human EEG and MEG recording, brain stimulation methods, and analysis of syndromes resulting from brain damage. We highlight the strengths and weaknesses of these methods to demonstrate how these techniques must be used in a complementary manner. We want our readers to learn what questions to ask, how to choose the tools and design experiments to answer these questions, and how to evaluate and interpret the results of those experiments. Despite the amazing progress of the neurosciences, the brain remains a great mystery, with each insight inspiring new questions. For this reason, we have not used a declarative style of writing throughout the book. Instead, we tend to present results that can be interpreted in more than one way, helping the reader to recognize that there are possible alternative interpretations.

Since the first edition, there have been many major developments, both methodological and theoretical. There has been an explosion of brain imaging studies—almost 1,500 a year for the last decade. New technologies, such as transcranial magnetic stimulation, diffusion tensor imaging and optogenetics have been added to the arsenal of the cognitive neuroscientist. New links to genetics, comparative anatomy, computation and robotics have emerged. Parsing all of these studies and deciding which ones should be included has been a major challenge for us. We firmly believe that technology is a cornerstone of scientific advancement. As such, we have felt it essential to capture the cutting-edge trends in the field, while keeping in mind that this is an undergraduate survey text that needs to be completed in a quarter or semester.

The first three editions have provided compelling evidence that our efforts have led to a highly useful text for undergraduates taking their first course in cognitive neuroscience, as well as a concise reference volume for graduate students and researchers. Over 400 colleges and universities worldwide have adopted the text. Moreover, instructors tell us that in addition to our interdisciplinary approach, they like that our book has a strong narrative voice and offers a manageable number of chapters to teach in a one-semester survey course.

Still, we have had to do some pruning for the 4th edition in order to present both the foundations of cognitive neuroscience and the latest the field has to offer; in general, we have opted to take a leaner approach than in previous editions, providing the necessary updates on new developments while streamlining the descriptions of experimental results. Inspired by feedback from our adopters, we have also made some changes to make the text even more user friendly. Highlights of the fourth edition include the following:

- All the chapters have been rewritten. In order to add new findings but maintain a reasonable sized text, we had to trim out some of the older material and streamline our presentations. Careful attention has been paid to the chapter's heading and subheading structure to provide a roadmap to the essential themes of the chapters.
- The illustrations have been redrawn. The stunning new art program is designed to facilitate student understanding, and now includes a "hand-pointer" feature that draws students' attention to the most important figure elements.
- We have added an "anatomical orientation" figure at the beginning of each chapter to orient students to the brain regions that will be major players throughout the chapter.
- Key points to remember have been interspersed after major sections throughout the text instead of being stacked at the end of the chapter.
- The chapters on cellular mechanisms and neuroanatomy have been combined, providing a concise presentation of the basic concepts that are most essential for cognitive neuroscience. The focus of the field is more at the systems level of analysis, and this has led us to leave the more detailed study of cellular and molecular topics to texts dedicated to these levels of analysis.
- We have eliminated the chapter on the evolutionary perspective and instead have sprinkled discussions of this topic throughout the text.
- An extensive section on decision-making has been added to the cognitive control chapter.
- The chapter on emotion has been expanded and includes extensive discussion of the fine interplay between affective and cognitive neurosciences.
- We have added a new chapter that tackles the important, yet elusive problem of consciousness, taking on issues such as free will and how cognitive neuroscience can have practical applications for informing public policy and the law.

The new edition also offers an even more generous suite of instructor ancillaries:

- Lecture PowerPoints, new to this edition, feature text and images as well as instructor-only lecture notes and suggestions.
- Art PowerPoints and JPEGs provide all the art and tables from the book in easily adaptable formats.
- The Test Bank for *Cognitive Neuroscience*, Fourth Edition, has been developed using the Norton Assessment Guidelines. Each chapter of the Test Bank includes five question types classified according to the first five levels of Bloom's taxonomy of knowledge types.
- The Studying the Mind DVD includes exclusive Norton interviews with leading cognitive neuroscience researchers on key aspects of how we study the human mind.
- The Cognitive Neuroscience Patient Interviews DVD presents original footage of interviews with patients suffering from a variety of cognitive and neurological disorders, and bring to life the cognitive models, concepts, and research methodologies discussed in the text. Several new videos have been added for the fourth edition.

As with each edition, this book has required a laborious interactive effort among the three of us, along with extensive discussions with our colleagues, our students, and our reviewers. The product has benefited immeasurably from these interactions. Of course we are ready to modify and improve any and all of our work. In our earlier editions, we asked readers to contact us with suggestions and questions, and we do so again. We live in an age where interaction is swift and easy. We are to be found as follows: gazzaniga@psych.ucsb.edu; mangun@ucdavis.edu; ivry@socrates.berkeley.edu.

Good reading and learning!

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Once again, we are indebted to a number of people. First and foremost we would like to thank Rebecca A. Gazzaniga, M.D. for her extensive and savvy editing of the Fourth Edition. She mastered every chapter, with an eye to make sure the story was clear and engaging. We could not have completed this edition without her.

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Often we forget to thank the many people, some of whom have generously given hundreds of hours of their time, for being participants in the research work that we discuss; without their contributions, cognitive neuroscience would not be where it is today.

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FOURTH EDITION

Cognitive Neuroscience

The Biology of the Mind

In science it often happens that scientists say, "You know that's a really good argument; my position is mistaken," and then they actually change their minds and you never hear that old view from them again. They really do it. It doesn't happen as often as it should, because scientists are human and change is sometimes painful. But it happens every day. I cannot recall the last time something like that happened in politics or religion.

~Carl Sagan, 1987

A Brief History of Cognitive Neuroscience

chapter

1

OUTLINE

A Historical Perspective

The Brain Story

The Psychological Story

The Instruments of Neuroscience

The Book in Your Hands

AS ANNE GREEN WALKED to the gallows in the castle yard of Oxford, England, in 1650, she must have been feeling scared, angry, and frustrated. She was about to be executed for a crime she had not committed: murdering her stillborn child. Many thoughts raced through her head, but "I am about to play a role in the founding of clinical neurology and neuroanatomy" although accurate, certainly was not one of them. She proclaimed her innocence to the crowd, a psalm was read, and she was hanged. She hung there for a full half hour before she was taken down, pronounced dead, and placed in a coffin provided by Drs. Thomas Willis and William Petty. This was when Anne Green's luck began to improve. Willis and Petty were physicians and had permission from King Charles I to dissect, for medical research, the bodies of any criminals killed within 21 miles of Oxford. So, instead of being buried, Anne's body was carried to their office.

An autopsy, however, was not what took place. As if in a scene from Edgar Allan Poe, the coffin began to emit a grumbling sound. Anne was alive! The doctors poured spirits in her mouth and rubbed a feather on her neck to make her cough. They rubbed her hands and feet for several minutes, bled five ounces of her blood, swabbed her neck wounds with turpentine, and cared for her through the night. The next morning, able to drink fluids and feeling more chipper, Anne asked for a beer. Five days later, she was out of bed and eating normally (Molnar, 2004; Zimmer, 2004).

After her ordeal, the authorities wanted to hang Anne again. But Willis and Petty fought in her defense, arguing that her baby had been stillborn and its death was not her fault. They declared that divine providence had stepped in and provided her miraculous escape from death, thus proving her innocence. Their arguments prevailed. Anne was set free and went on to marry and have three more children.

This miraculous experience was well publicized in England (Figure 1.1). Thomas Willis (Figure 1.2) owed much to Anne Green and the fame brought to him by the events of her resurrection. With it came money he desperately needed and the prestige to publish his work and disseminate his ideas, and he had some good ones. An inquisitive neurologist, he actually coined the term *neurology* and became one of the best-known doctors of his time. He was the first anatomist to link abnormal human behaviors to changes in brain structure. He drew these conclusions after treating patients throughout their

FIGURE 1.1 An artistic rendition of the miraculous resurrection of Anne Green in 1650.

lives and autopsying them after their deaths. Willis was among the first to link specific brain damage to specific behavioral deficits, and to theorize how the brain transfers information in what would later be called *neuronal conduction*.

With his colleague and friend Christopher Wren (the architect who designed St. Paul's Cathedral in London), Willis created drawings of the human brain that remained the most accurate representations for 200 years (Figure 1.3). He also coined names for a myriad of brain regions (Table 1.1; Molnar, 2004; Zimmer, 2004). In short, Willis set in motion the ideas and knowledge base that took hundreds of years to develop into what we know today as the field of *cognitive neuroscience*.

In this chapter, we discuss some of the scientists and physicians who have made important contributions to this field. You will discover the origins of cognitive neuroscience and how it has developed into what it is today: a discipline geared toward understanding how the brain works, how brain structure and function affect behavior, and ultimately how the brain enables the mind.

A Historical Perspective

The scientific field of **cognitive neuroscience** received its name in the late 1970s in the back seat of a New York City taxi. One of us (M.S.G.) was riding with the great cognitive psychologist George A. Miller on the way to a dinner meeting at the Algonquin Hotel. The dinner was being held for scientists from Rockefeller and Cornell universities, who were joining forces to study how the brain enables the mind—a subject in need of a name. Out of that taxi ride came the term *cognitive neuroscience*—from *cognition*, or the process of knowing (i.e., what arises from awareness, perception, and reasoning), and *neuroscience* (the study of how the nervous system is organized and functions). This seemed the perfect term to describe the question of understanding how the functions of the physical brain can yield the thoughts and ideas of an intangible mind. And so the term took hold in the scientific community.

FIGURE 1.2 Thomas Willis (1621–1675), a founder of clinical neuroscience.

When considering the miraculous properties of brain function, bear in mind that Mother Nature built our brains through the process of evolution; they were not designed by a team of rational engineers. While life first appeared on our 4.5-billion-year-old Earth approximately 3.8 billion years ago, human brains, in their present form, have been around for only about 100,000 years, a mere drop in the bucket. The primate brain appeared between 34 million and 23 million years ago, during the Oligocene epoch. It evolved into the progressively larger brains of the great apes in the Miocene epoch between roughly 23 million and 7 million years ago. The human

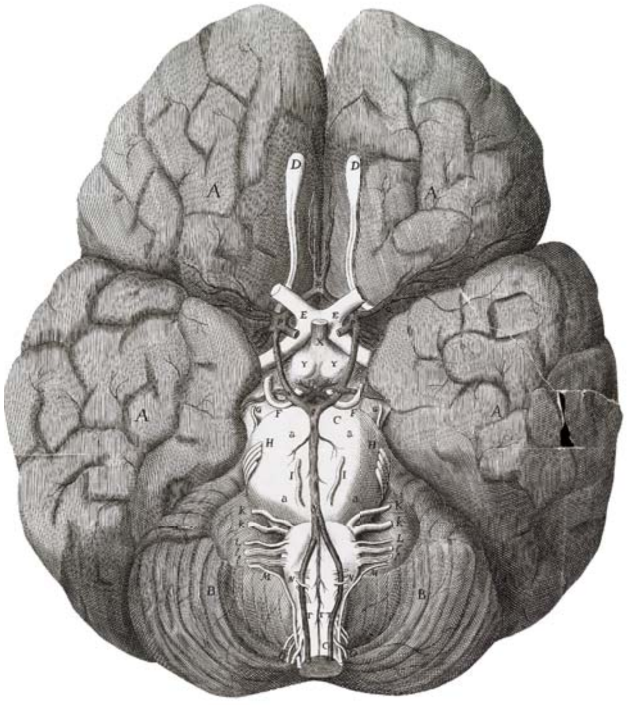


FIGURE 1.3 The human brain (ventral view) drawn by Christopher Wren for Thomas Willis, published in Willis's *The Anatomy of the Brain and Nerves*.

TABLE 1.1 A Selection of Terms Coined by Thomas Willis

Term	Definition
Anterior commissure	Axonal fibers connecting the middle and inferior temporal gyri of the left and right hemispheres.
Cerebellar peduncles	Axonal fibers connecting the cerebellum and brainstem.
Claustrum	A thin sheath of gray matter located between two brain areas: the external capsule and the putamen.
Corpus striatum	A part of the basal ganglia consisting of the caudate nucleus and the lenticular nucleus.
Inferior olives	The part of the brainstem that modulates cerebellar processing.
Internal capsule	White matter pathways conveying information from the thalamus to the cortex.
Medullary pyramids	A part of the medulla that consists of corticospinal fibers.
Neurology	The study of the nervous system and its disorders.
Optic thalamus	The portion of the thalamus relating to visual processing.
Spinal accessory nerve	The 11th cranial nerve, which innervates the head and shoulders.
Stria terminalis	The white matter pathway that sends information from the amygdala to the basal forebrain.
Striatum	Gray matter structure of the basal ganglia.
Vagus nerve	The 10th cranial nerve, which, among other functions, has visceral motor control of the heart.

lineage diverged from the last common ancestor that we shared with the chimpanzee somewhere in the range of 5–7 million years ago. Since that divergence, our brains have evolved into the present human brain, capable of all sorts of wondrous feats. Throughout this book, we will be reminding you to take the evolutionary perspective: Why might this behavior have evolved? How could it promote survival and reproduction? WWHGD? (What would a hunter-gather do?) The evolutionary perspective often helps us to ask more informed questions and provides insight into how and why the brain functions as it does.

During most of our history, humans were too busy to think about thought. Although there can be little doubt that the brains of our long-ago ancestors could engage in such activities, life was given over to more practical matters, such as surviving in tough environments, developing ways to live better by inventing agriculture or domesticating animals, and so forth. Nonetheless, the brain mechanisms that enable us to generate theories about the characteristics of human nature thrived inside the heads of ancient humans. As civilization developed to the point where day-to-day survival did not occupy every hour of every day, our ancestors began to spend time looking for causation and constructing complex theories about the motives of fellow humans. Examples of attempts to understand the world and our place in it include *Oedipus Rex* (the ancient Greek play that deals with the nature of the child–parent conflict) and Mesopotamian and Egyptian theories on the nature of religion and the universe. Although the pre-Socratic Greek philosopher, Thales, rejected supernatural explanations of phenomena and proclaimed that every event had a natural cause (presaging modern cognitive neuroscience), the early Greeks had one big limitation: They did not have the methodology to explore the mind systematically through experimentation.

It wasn't until the 19th century that the modern tradition of observing, manipulating, and measuring became the norm, and scientists started to determine how the brain gets its jobs done. To understand how biological systems work, a laboratory is needed and experiments have to be performed to answer the questions under study and to support or refute the hypotheses and conclusions that have been made. This approach is known as the scientific method, and it is the only way that a topic can move along on sure footing. And in the case of cognitive neuroscience, there is no end to the rich phenomena to study.

The Brain Story

Imagine that you are given a problem to solve. A hunk of biological tissue is known to think, remember, attend, solve problems, tell jokes, want sex, join clubs, write novels, exhibit bias, feel guilty, and do a zillion other things. You are supposed to figure out how it works. You might start by looking at the big picture and asking yourself a couple of questions. "Hmmm, does the blob work as a unit with each part contributing to a whole? Or, is the blob full of individual processing parts, each carrying out specific functions, so the result is something that looks like it is acting as a whole unit?" From a distance the city of New York (another type of blob) appears as an integrated whole, but it is actually composed of millions of individual processors—that is, people. Perhaps people, in turn, are made of smaller, more specialized units.

This central issue—whether the mind is enabled by the whole brain working in concert or by specialized parts of the brain working at least partly independently—is what fuels much of modern research in cognitive neuroscience.

FIGURE 1.4 Franz Joseph Gall (1758–1828), one of the founders of phrenology.

As we will see, the dominant view has changed back and forth over the years, and it continues to change today.

Thomas Willis foreshadowed cognitive neuroscience with the notion that isolated brain damage (biology) could affect behavior (psychology), but his insights slipped from view. It took another century for Willis's ideas to resurface. They were expanded upon by a young Austrian physician and neuroanatomist, Franz Joseph Gall (Figure 1.4). After studying numerous patients, Gall became convinced that the brain was the organ of the mind and that innate faculties were localized in specific regions of the cerebral cortex. He thought that the brain was organized around some 35 or more specific functions, ranging from cognitive basics such as language and color perception to more ephemeral capacities such as affection and a moral sense, and each was supported by specific brain regions. These ideas were well received, and Gall took his theory on the road, lecturing throughout Europe.

Building on his theories, Gall and his disciple Johann Spurzheim hypothesized that if a person used one of the faculties with greater frequency than the others, the part of the brain representing that function would grow (Gall & Spurzheim, 1810–1819). This increase in local brain size would cause a bump in the overlying skull. Logically, then, Gall and his colleagues believed that a careful analysis of the skull could go a long way in describing the personality of the person inside the skull. Gall called this technique *anatomical personology* (Figure 1.5). The idea that character could be divined through palpating the skull was dubbed **phrenology** by Spurzheim and, as you may well imagine, soon fell into the hands of charlatans. Some employers even required job applicants to have their skulls "read" before they were hired.

Gall, apparently, was not politically astute. When asked to read the skull of Napoleon Bonaparte, Gall did not ascribe to his skull the noble characteristics that the future emperor was quite sure he possessed. When Gall later applied to the Academy of Science of Paris, Napoleon decided that phrenology needed closer scrutiny and ordered the Academy to obtain some scientific evidence of its validity. Although Gall was a physician and neuroanatomist, he was not a scientist. He observed correlations and sought only to confirm, not disprove, them. The Academy asked physiologist Marie-Jean-Pierre Flourens (Figure 1.6) to see if he could come up with any concrete findings that could back up this theory.

Flourens set to work. He destroyed parts of the brains of pigeons and rabbits and observed what happened. He was the first to show that indeed certain parts of the brain were responsible for certain functions. For instance, when he removed the cerebral hemispheres, the animal no longer had perception, motor ability, and judgment.

a b c

FIGURE 1.5 **(a)** An analysis of Presidents Washington, Jackson, Taylor, and McKinley by Jessie A. Fowler, from the *Phrenological Journal*, June 1898. **(b)** The phrenological map of personal characteristics on the skull, from the *American Phrenological Journal*, March 1848. **(c)** Fowler & Wells Co. publication on marriage compatibility in connection with phrenology, 1888.


a

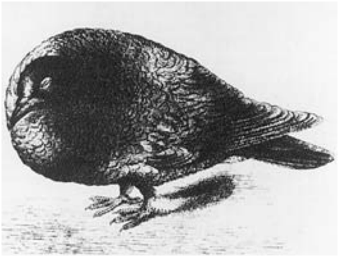

b

FIGURE 1.6 **(a)** Marie-Jean-Pierre Flourens (1794–1867), who supported the idea later termed the *aggregate field theory*. **(b)** The posture of a pigeon deprived of its cerebral hemispheres, as described by Flourens.

Without the cerebellum, the animals became uncoordinated and lost their equilibrium. He could not, however, find any areas for advanced abilities such as memory or cognition and concluded that these were more diffusely scattered throughout the brain. Flourens developed the notion that the whole brain participated in behavior, a view later known as the **aggregate field theory**. In 1824, Flourens wrote, "All sensations, all perceptions, and all volitions occupy the same seat in these (cerebral) organs. The faculty of sensation, percept and volition is then essentially one faculty." The theory of localized brain functions, known as localizationism, fell out of favor.

That state of affairs didn't last for too long, however. New evidence obtained through clinical observations and autopsies started trickling in from across Europe, and it helped to swing the pendulum slowly back to the localizationist view. In 1836 a neurologist from Montpellier, Marc Dax, provided one of the first bits of evidence. He sent a report to the Academy of Sciences about three patients, noting that each had speech disturbances and similar left-hemisphere lesions found at autopsy. At the time, a report from the provinces got short shrift in Paris, and it would be another 30 years before anyone took much notice of this observation that speech could be disrupted by a lesion to one hemisphere only.

FIGURE 1.7 John Hughlings Jackson (1835–1911), an English neurologist who was one of the first to recognize the localizationist view.

Meanwhile, in England, the neurologist John Hughlings Jackson (Figure 1.7) began to publish his observations on the behavior of persons with brain damage. A key feature of Jackson's writings was the incorporation of suggestions for experiments to test his observations. He noticed, for example, that during the start of their seizures, some epileptic patients moved in such characteristic ways that the seizure appeared to be stimulating a set map of the body in the brain; that is, the clonic and tonic jerks in muscles, produced by the abnormal epileptic firings of neurons in the brain, progressed in the same orderly pattern from one body part to another. This phenomenon led Jackson to propose a *topographic* organization in the cerebral cortex—that is, a map of the body was represented across a particular cortical area, where one part would represent the foot, another the lower leg, and so on. As we will see, this proposal was verified over a half century later by Wilfred Penfield. Jackson was one of the first to realize this essential feature of brain organization.

Although Jackson was also the first to observe that lesions on the right side of the brain affect visuospatial processes more than do lesions on the left side, he did not maintain that specific parts of the right side of the brain were solely committed to this important human cognitive function. Being an observant clinical neurologist, Jackson noticed that it was rare for a patient to lose a function completely. For example, most people who lost their capacity to speak following a cerebral stroke could still say some words. Patients unable to direct their hands voluntarily to specific places on their bodies could still easily scratch those places if they itched. When Jackson made these observations, he concluded that many regions of the brain contributed to a given behavior.

Meanwhile, the well-known and respected Parisian physician Paul Broca (Figure 1.8a) published, in 1861, the results of his autopsy on a patient who had been nicknamed Tan—perhaps the most famous neurological case in history. Tan had developed aphasia: He could understand language, but "tan" was the only word he could utter. Broca found that Tan (his real name was Leborgne) had a syphilitic lesion in his left hemisphere in the inferior frontal lobe. This region of the brain has come to be called *Broca's area.* The impact of this finding was huge. Here was a specific aspect of language that was impaired by a specific lesion. Soon Broca had a series of such patients. This theme was picked up by the German neurologist Carl Wernicke. In 1876, Wernicke reported on a stroke victim who (unlike Broca's patient) could talk quite freely but made little sense when he spoke. Wernicke's patient also could not understand spoken or written language. He had a lesion in a more posterior region of the left hemisphere, an area in and around where the temporal and parietal lobes meet, which is now referred to as *Wernicke's area* (Figure 1.8b).

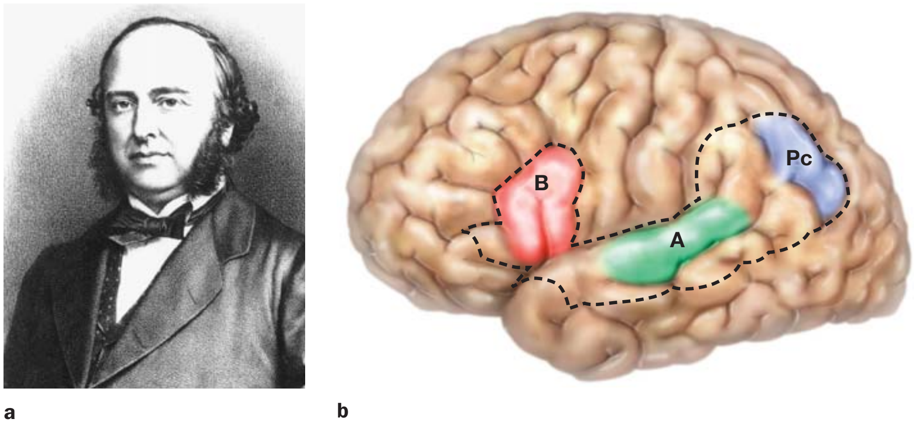


FIGURE 1.8 **(a)** Paul Broca (1824–1880). **(b)** The connections between the speech centers, from Wernicke's 1876 article on aphasia. A = Wernicke's sensory speech center; B = Broca's area for speech; Pc = Wernicke's area concerned with language comprehension and meaning.

Today, differences in how the brain responds to focal disease are well known (H. Damasio et al., 2004; R. J. Wise, 2003), but a little over 100 years ago Broca's and Wernicke's discoveries were earth-shattering. (Note that people had largely forgotten Willis's observations that isolated brain damage could affect behavior. Throughout the history of brain science, an unfortunate and oft repeated trend is that we fail to consider crucial observations made by our predecessors.) With the discoveries of Broca and Wernicke, attention was again paid to this startling point: Focal brain damage causes specific behavioral deficits.

As is so often the case, the study of humans leads to questions for those who work on animal models. Shortly after Broca's discovery, the German physiologists Gustav Fritsch and Eduard Hitzig electrically stimulated discrete parts of a dog brain and observed that this stimulation produced characteristic movements in the dog. This discovery led neuroanatomists to more closely analyze the cerebral cortex and its cellular organization; they wanted support for their ideas about the importance of local regions. Because these regions performed different functions, it followed that they ought to look different at the cellular level.

Following this logic, German neuroanatomists began to analyze the brain by using microscopic methods to view the cell types in different brain regions. Perhaps the most famous of the group was Korbinian Brodmann, who analyzed the cellular organization of the cortex and characterized 52 distinct regions (Figure 1.9). He published his cortical maps in 1909. Brodmann used tissue stains, such as the one developed by Franz Nissl, that permitted him to visualize the different cell types in different brain regions. How cells differ between brain regions is called **cytoarchitectonics**, or *cellular architecture.*

Soon many now-famous anatomists, including Oskar Vogt, Vladimir Betz, Theodor Meynert, Constantin von

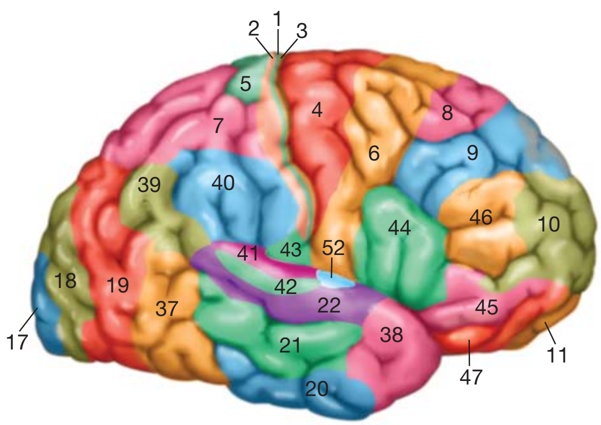


FIGURE 1.9 Sampling of the 52 distinct areas described by Brodmann on the basis of cell structure and arrangement.

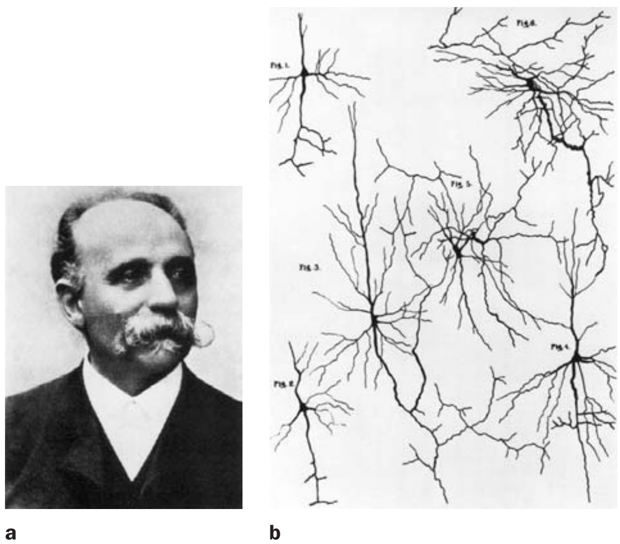


FIGURE 1.10 **(a)** Camillo Golgi (1843–1926), cowinner of the Nobel Prize in 1906. **(b)** Golgi's drawings of different types of ganglion cells in dog and cat.

Economo, Gerhardt von Bonin, and Percival Bailey, contributed to this work, and several subdivided the cortex even further than Brodmann had. To a large extent, these investigators discovered that various cytoarchitectonically described brain areas do indeed represent functionally distinct brain regions. For example, Brodmann first distinguished area 17 from area 18—a distinction that has proved correct in subsequent functional studies. The characterization of the primary visual area of the cortex, area 17, as distinct from surrounding area 18, remarkably demonstrates the power of the cytoarchitectonic approach, as we will consider more fully in Chapter 2.

Despite all of this groundbreaking work in cytoarchitectonics, the truly huge revolution in our understanding of the nervous system was taking place elsewhere, in Italy and Spain. There, an intense struggle was going on between two brilliant neuroanatomists. Oddly, it was the work of one that led to the insights of the other. Camillo Golgi (Figure 1.10), an Italian physician, developed one of the most famous cell stains in the history of the world: the silver method for staining neurons—*la reazione nera*, “the black reaction,” that impregnated individual neurons with silver chromate. This stain permits visualization of individual neurons in their entirety. Using Golgi’s method, Santiago Ramón y Cajal (Figure 1.11) went on to find that, contrary to the view of Golgi and others, neurons were discrete entities. Golgi had believed that the whole brain was a **syncytium**, a continuous mass of tissue that shares a common cytoplasm. Ramón y Cajal, who some call the father of modern neuroscience, was the first to identify the unitary nature of neurons and to articulate what came to be known as the **neuron doctrine**, the concept that the nervous system is made up of individual cells. He also recognized that the transmission of electrical information went in only one direction, from the dendrites down to the axonal tip (Figure 1.12).

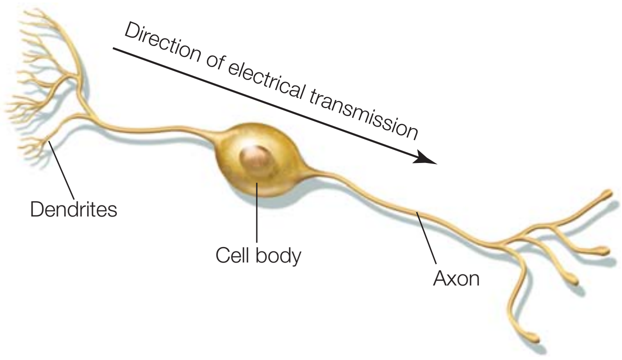
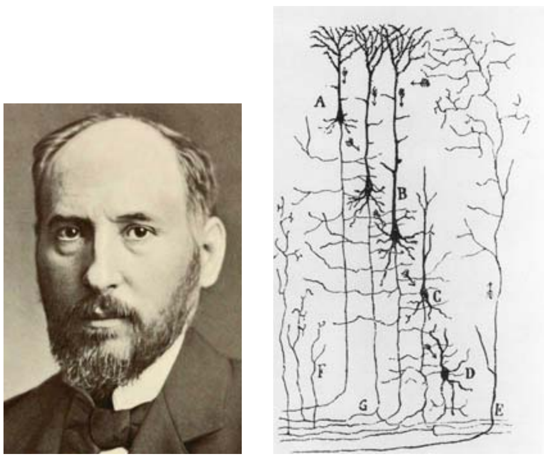


FIGURE 1.12 A bipolar retinal cell, illustrating the dendrites and axon of the neuron.

Many gifted scientists were involved in the early history of the neuron doctrine (Shepherd, 1991). For example, Jan Evangelista Purkinje (Figure 1.13), a Czech, not only described the first nerve cell in the nervous system in 1837 but also invented the stroboscope, described common visual phenomena, and made



a b

FIGURE 1.11 **(a)** Santiago Ramón y Cajal (1852–1934), cowinner of the Nobel Prize in 1906. **(b)** Ramón y Cajal’s drawing of the afferent inflow to the mammalian cortex.

a b

FIGURE 1.13 **(a)** Jan Evangelista Purkinje (1787–1869), who described the first nerve cell in the nervous system. **(b)** A Purkinje cell of the cerebellum.